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The Genus *Xironogiton* Ellis, 1919 (Clitellata: Branchiobdellida)

Abstract—Holt, Perry C. The Genus *Xironogiton* Ellis, 1919 (Clitellata: Branchiobdellida). *Virginia Journal of Science* [Vol. 25, 5–19 (1974)]. Five species of the genus *Xironogiton*, three newly described, are recognized. One formerly recognized nominal species is reduced to synonomy. The present center of speciation in the genus is the Pacific northwest. The presence of *X. instabilis* in the mountains of the eastern United States argues for the antiquity of the order Branchiobdellida and its contained genera, since *Xironogiton* cannot be considered as primitive and *X. instabilis*, at least, reached the Pacific drainage before the present barriers between east and west came into existence. The hypothesis that the order differentiated in the southern Appalachians is not invalidated by this unusual distributional pattern which does not correspond to that of the hosts: several species of cambarid crayfishes of the genera *Cambarus* and *Orconectes* in the east and species of the astacid genus *Pacifastacus* in the west.

The accumulation of a large amount of material over the past twenty-five years makes it possible to offer an account of the systematics, evolution and zoögeographical relationships of the genus *Xironogiton* Ellis, 1919, as one of a continuing series of studies of the North American members of the order Branchiobdellida. Such is the purpose of this paper.

Following a summary of the history of the knowledge of the genus, the methods and materials are described and some comments on the ecology of the members of the genus are presented. Taxonomic characteristics of the branchiobdellids have been rather fully discussed in the past (Holt, 1953, 1960, 1968c, Hoffman, 1963), but a brief review of taxonomically important characters, with emphasis on those peculiar to the genus, is given. The evolutionary and distributional relationships of the genus are obscure and hypotheses that deal with these questions are difficult to formulate, but tentative ones are considered. An emended diagnosis of the genus is followed by a key to its component species. Of the five species recognized, three are newly described and one previously described species composed of two subspecies (Ellis, 1919: 249–251), reduced to the status of a subspecies by Goodnight (1940:47), is synonomyzed with a previously recognized species (Moore, 1894:425–427). All species are diagnosed, fully described (or former descriptions emended), illustrated, locality data and the disposition of materials given, their hosts recorded (if possible) and their distributions plotted on a map.

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Review of the Literature

Our knowledge of the genus *Xironogiton* begins with the publication of the description of *Branchiobdella instabilia* (Moore, 1894:425–497) from Watauga County, North Carolina. Smallwood (1906) discussed what was known in his time of the natural history of branchiobdellids, concentrating on *Br. instabilia,* and studied gametogenesis in this species. He was the first, to my knowledge, to call attention to the fact that most branchiobdellids are not parasitic. Pierantoni (1912:22), in his short monograph of the order (then considered a family of the Oligochaeta) assigned *Br. instabilia* (as *instabilis*) to the genus *Bdellodrilus* Moore, 1895, without apparently, having seen any specimens of the species. Similarly, Hall (1914:190, 192) lists *Bd. instabilis* in a key and quotes Moore's records. Ellis (1912: 248) included *Br. instabilia* in a key to the branchiobdellids of eastern North America. Later, he (1919: 247) erected the genus *Xironogiton* for three species and one subspecies: *X. oregonensis oregonensis* Ellis, designated as the type species, *X. o. pectinatus* Ellis, *X. occidentalis* Ellis and *X. instabilius* Moore. Stephenson (1930:802) listed *Xironogiton* among the genera of the branchiobdellids. Goodnight (1940: 43–48) emended the proviously presented generic diagnoses, reduced *X. oregonensis* to the status of a subspecies of *X. instabilius*, quoted extensively from the descriptions of Moore (1894) and Ellis (1919) of all the nominal species and added a few locality records. The reproductive systems of *X. instabilius* were studied by Holt (1949) and compared with those of *Cambarincola philadelphicus* (Leidy, 1851). Holt (1951:198-119) further considered very briefly our knowledge of the genus and commented upon Ellis's types of *X. oregonensis*. Berry and Holt (1959) studied the responses of *X. instabilius* (and *Xironodrilus formosus* Ellis, 1918) to experimentally produced changes in temperature and oxygen tensions. McManus (1960) studied the ecology of *X. instabilius* in New York. Brown (1961) recorded observations on the ecology and microhabitat on the host of a population of the species in Virginia. Franzén (1962) wrote on the histology of the muscles. Hobbs, Holt and Walton (1967) included this species in their study of the crayfishes and their epizoötic associates of the Mountain Lake, Virginia, region. Holt (1968a) summarized the ecological knowledge of the species, commented on its distribution and pointed out that *X. i. instabilius* and *X. i. oregonensis* are at present indistinguishable. In another paper (Holt, 1969), the distribution of *X. instabilius* in the southern Appalachians and the relationship of the genus to other genera of the order were discussed.

Three nominal species of branchiobdellids from Lake Dojran, Yugoslavia, were assigned to *Xironogiton* by Georgévitch (1955): *X. bidens, X. dilatus, X. dolicoderos*. Later (1957), he added *X. tridens* and *X. latus* to the list of Jugoslavian branchiobdellids. Pop (1965:237) reduced all of these names proposed by Georgévitch to synonomy as follows: *Xironogiton bidens* Georgévitch, 1955, to synonomy with *Branchiobdella parasita* Henle, 1835; *Xironogiton dilatus* Georgévitch, 1955, *Xironogiton dolicoderos* Georgévitch, 1955, *Xironogiton latus* Georgévitch, 1957, and *Xironogiton tridens* Georgévitch, 1957, all to synonomy with *Branchiobdella pentodonta* Whitman, 1882. Specimens referred to *Xironogiton dolicoderos* by Georgévitch (1957) were described as *Branchiobdella pentodonta orientalis* Pop, 1965. There is not any doubt of Pop's correctness in referring Georgévitch's Macedonian worms to the genus *Branchiobdella*. There remains, then, only the North American species to consider in treating the genus *Xironogiton*.

Other than casual mention in papers primarily devoted to other genera (*e.g.* Holt, 1967), mention in textbooks and generalized compendia (*e.g.* Pennak, 1953) and, possibly, in papers by others not primarily devoted to branchiobdellids that may have been overlooked, nothing else has been written about the genus *Xironogiton*.

Methods and Disposition of Materials

The general methods used in the taxonomic study of the branchiobdellids have been described before (Holt, 1960:67; and other papers). The taxonomically more significant structures are labelled (Figure 5). The serial sections were prepared according to standard paraffin embedding methods, sectioned at ten microns, stained with Delafield's hematoxylin and counter-stained in eosin. The use of a 40X fluorite oil immersion objective, corrected to a working distance of 1.5 mm, makes it possible to study specimens mounted entire from both sides. Some very large (for branchiobdellids) specimens lend themselves profitably to dissection with fine needles. All drawings are so oriented that the anterior of the animal, or part thereof, is to the reader's right. Measurements, made with a calibrated ocular micrometer, are to be regarded as approximations and are given to the nearest 0.1 mm. Numbers in parentheses following the average size of a dimension represent the range in size of the animals, or parts thereof, measured. The greatest width given is always that of segment VII.

Most of the material upon which this paper is based is deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNM); some paratypes and reference specimens are retained in my collections at the Virginia Polytechnic Institute and State University (PCH). In all cases complete locality data, if not given herein, are available from my files or from the Registrar, National Museum of Natural History, Smithsonian Institution.

Evolutionary and Zoögeographical Considerations

The evolutionary relationships of the genus *Xironogiton* and its members present difficult problems, some of which have been considered briefly (Holt, 1964:260; 1968a:38–34; 1969:196–197). I shall review the tentative conclusions of these papers. The distributional pattern of the members of the genus, which has been touched upon in the papers cited immediately above, is a more difficult problem involving the hosts and their other epizoötic associates, the entocytherid ostracods, and serious uncertainties concerning the geology of the region. I shall consider first the phylogentic relationships of the genus and its constituent species.

In the almost total absence of a fossil record of any of these three groups (freshwater astacids are presumed to have been in existence since at least late Mesozoic times and North American fossils are known from Tertiary beds of Idaho and Wyoming, Hobbs, personal communication)—the crayfishes, the entocytherid ostracods and the branchiobdellids, that seem to form an indissoluble symbiotic assemblage, but with limited, if any host species specificity —one is perforce constrained to postulate separate phylogenetic hypotheses for each based upon the more or less uncertain grounds of morphological affinities.

Four genera (*Cirrodrilus* Pierantoni, 1905; *Ankyrodrilus* Holt, 1965, *Xironogiton* Ellis, 1919; *Branchiobdella* Odier, 1823) are characterized by two anterior nephridopores, the entry of the vasa deferentia into the spermiducal gland ectal to its ental end and the absence of a prostate or prostatic protuberance. They are related to, but nonetheless, in localized areas with species of *Cambarincola*, the *Bdellodrilus* Moore, 1895, which have only one anterior nephridiopore.

Of this group of genera, the *Cirrodrilus*-lineage, *Cirrodrilus* is Asiatic and has a completely eversible penis and on this basis has to be considered as primitive. *Branchiobdella,* European and east Asian in distribution, likewise has an eversible penis but has lost a pair of testes in segment V. The American *Ankyrodrilus* is represented by two southern Appalachian species with a bursa composed of a very large penial sheath region that appears to be eversible and to carry, as a protrusible cone, the penis with it when everted (Holt, 1965). *Xironogiton,* with a large, muscular bursa and a protrusible penis, and the movement of the vasa deferentia to or near the junction of the spermiducal gland and the ejaculatory duct must be considered as an advanced member of the lineage. In addition, the "somatic" (non-genitalic) characters and the microniche occupied on their hosts are advanced characteristics of the members of the genus *Xironogiton.* All members of the genus are specialized for an existence on the exposed surfaces of the chelipeds or carapace of their hosts by a flattening of the body. *Xironogiton occidentalis,* a species, the members of which are among the largest of known branchiobdellids, has a body that gradually widens to its greatest extent in segment VII (resembling markedly the otherwise distantly related members of the genus *Xironodrilus* in this respect); the other species of *Xironogiton* (except *X. cassiensis*) have terete anterior segments with a dramatic widening and flattening of the posterior ones and are small-to medium-sized members of the order. They all occupy the chelipeds of their hosts and as a group they are the most specialized members of the genus.

All anatomical evidence, however it is interpreted, and the adaptation to the exposed areas of the host indicate that *Xironogiton* is composed of advanced, specialized or more recently evolved species within its lineage, nevertheless the ranges of its species pose a difficult problem in historical zoögeography. *Xironogiton instabilis,* more specialized than *X. occidentalis,* is almost equally common (almost ubiquitous) in the colder mountain streams of the east and west (Figure 1). The other species (*X. fordi, X. cassiensis, X. kittitasi*) are all western, but are of apparently equal standing as advanced species. If one assumes the primitiveness within the genus of *X. occidentalis* as a grazer on the exposed carapace of the hosts, the other species could have arisen, in geographical isolation, by escaping competition for the resources furnished by the surface of the host's carapace in a retreat to the still more exposed and dangerous surfaces of the chelipeds of the hosts. In the east, species of the dominant genus *Cambarincola* and the less common, and perhaps now relict, members of *Xironodrilus* could have furnished such competition. In the west, *X. occidentalis,* itself, may have played such a competitive role *contra* its congeners, but it may, and appears to be, a geographical relict that has survived competition in localized areas with species of *Cambarincola,* the genus with the largest number of species of that region.

To summarize: *Xironogiton* arose as a genus in early, or at least by the Oligocene, Cenozoic times and underwent a very modest radiation as a group of species capable of living on the exposed upper surfaces of the host crayfish. This probably occurred (Holt 1968a:86) in the area now represented by the southern Appalachians and related uplands. If *X. occidentalis* is the most primitive species of the genus, it and the ancestors (*X. instabilis,* at the least) of its congeners were carried westward by the astacid progenitors of the crayfish genus *Pacifastacus* before the unknown time of the origin of an unsurmountable barrier for these animals between east and west. *X. instabilis* is confined to cold clear waters (Berry and Holt, 1959) and, in spite of its wide range, can be considered a relict species in the east. In the west, the reverse is true, it has available a greater number, almost the total Pacific drainage north of the Stanislaus River in California, of streams of favorable characteristics. In any case, the species, or its anatomically indistinguishable progenitor, is of great antiquity and is composed of two groups of populations that must, as two disjunct groups, have set some sort of record in maintaining their similarities without the remotest possibility of them exchanging genes across a barrier close to two thousand miles in width for a period of millions of years. An uncertain caveat to this conclusion must be entered on the basis of our ignorance of events in northern Canada in the interglacial times of the Pleistocene, or indeed, the conditions in northern Canada in pre-Pleistocene times, though the distinctness and distribution, to reemphasize, of the crayfish hosts minimize this warning.

The other species (*X. fordi, X. cassiensis, X. kittitasi*) most likely evolved in pockets of isolation produced by the tectonic and volcanic events of the Cenozoic from one or the other stocks (*X. occidentalis* and *X. instabilis*) already discussed. They could be either ancient or quite recent in origin; witness the apparent recent divergence of *Ceratodrilus thysanosomus* Hall, 1914, and *C. ophiorhysus* Holt, 1960 (Holt, 1960:58). Nothing more can be said: the history of the genus *Xironogiton* is blurred by the mists of astacid wanderings and evolution, the lack of host specificity, the vagaries of plate tectonics and consequent orogenies (McKenzie, 1972) and those of the Pleistocene and pre-Pleistocene climatic shifts.

Xironogiton Ellis, 1919

Type-species.—*Xironogiton oregonensis* Ellis, 1919:248, by original designation.

Diagnosis.—Medium to large branchiobdellids (known species from approximately 1.4 mm to 7.5 mm, preserved specimens, in length); body terete anteriorly, depressed posteriorly, without peristomial tentacles or dorsal projections on trunk segments, posterior sucker directed ventrad; jaws subrectangular; paired nephridiopores on dorsum of segment III; with two pairs of testes; spermiducal gland with vasa deferentia entering ectally; prostate or prostatic protuberance absent; ejaculatory duct present; penis protrusible, non-eversible; bursa large, heavily muscular, spherical, ellipsoid or asymmetri-

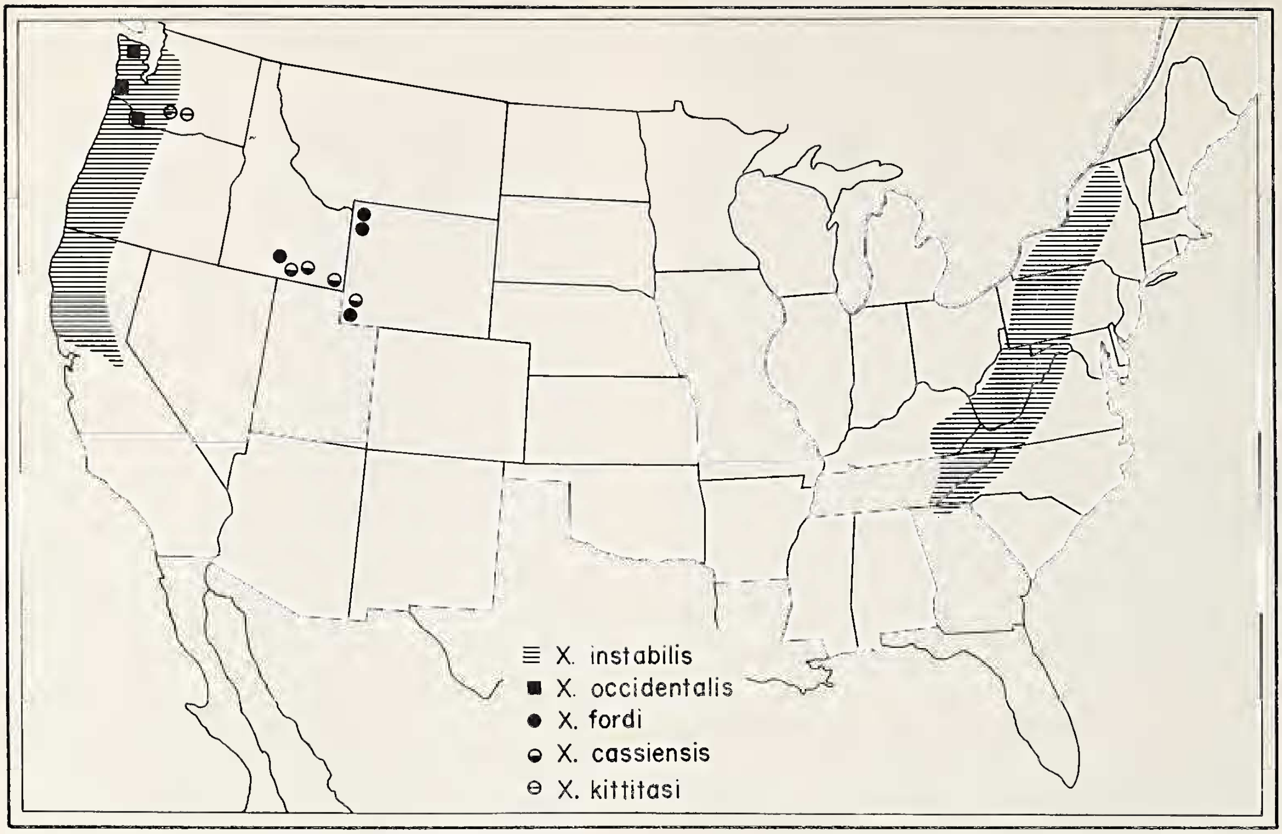

FIG. 1—Distribution of the species of the genus *Xironogiton*.

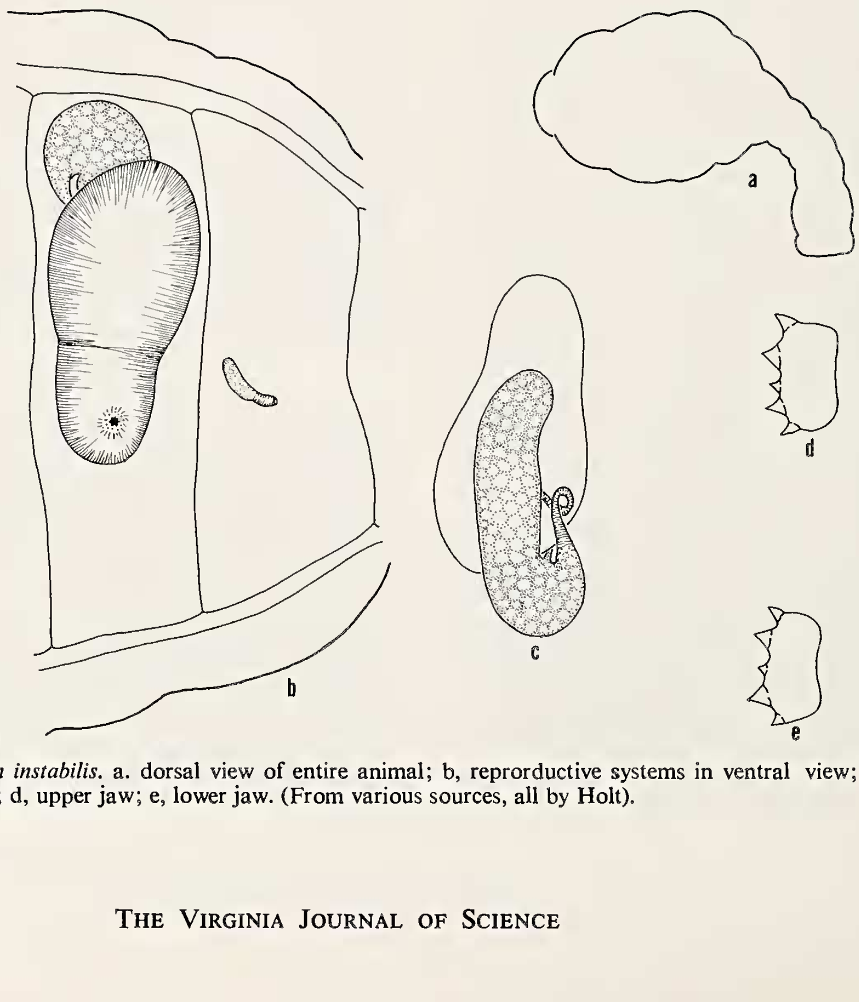

FIG. 2—*Xironogiton instabilis*. a. dorsal view of entire animal; b, reprorductive systems in ventral view; c. male reproductive system in dorsal view; d, upper jaw; e, lower jaw. (From various sources, all by Holt).

cally subpyriform; spermatheca disproportionately small.

Etymological note.—The name *Xironogiton* has been regarded as masculine and Ellis appears to have so intended when he used *pectinatus* as a name for what he thought was a subspecies of his *X. oregonensis.* A discussion of this point is important in an attempt to determine the correct form of the name of one of the species of the genus; the names applied to this species will be considered at the appropriate place below. An effort made by Dr. Thomas O. MacAdoo, Associate Professor of Foreign Languages, Virginia Polytechnic Institute and State University, to whom I am grateful, to determine more clearly the meaning and gender of the name *Xironogiton* revealed that the English of the Greek *giton* is "neighbor" and the word may be either masculine or feminine in Greek. *Xirono*— may have been derived from *Xyris* (= razor). Some credence is lent to these conjectures by virtue of the fact that Ellis (1919: 243) proposed the name *Xironodrilus* for a genus which he appears to have thought to be closely related to *Xironogiton* (Ellis, 1919:247). *Xironodrilus* can be translated loosely as "razor worm" (the members of this genus are flattened and a fanciful resemblance in shape, to a razor can be imagined) and *Xironogiton* as "neighbor to the razor." In any case, *Xironogiton* must be regarded as of Greek origin and as masculine in gender on the basis of Article 30, a1 and 2, of the International Code of Zoological Nomenclature, London, 1961, since Ellis did not indicate otherwise.

Key to the Species of the Genus *Xironogiton*

1 Teeth of subequal length, teeth-bearing margin of jaws linear ..... *Xironogiton fordi*

1′ Teeth of at least one jaw of unequal length, teeth-bearing margin of jaws variable.. 2

2(1′) Teeth-bearing margin of jaws concave; dental formula 6/6 to 7/7, body increasing gradually to greatest width, spermiducal gland long extending beyond mid-line of body .... *Xironogiton cassiensis*

2′ Teeth-bearing margin of jaws sublinear or convex, dental formula, spermiducal gland and body form variable 3

3(2′) Dental formula 4/4 to 11/11, segments V-VIII much broader than terete anterior segments, ental end of spermiducal gland rarely or never extending beyond mid-line of body .... *Xironogiton instabilis*

3′ Either very large worms (greater than 5.4 mm in length) with spermiducal gland looped laterally to bursa; or small worms (about 1.4 to 2.0 mm in length) with proportionately very long spermiducal gland lying transversally in segment dorsal to gut .. 4

4(3′) Teeth-bearing margin of jaws convex, dental formula 6/6, body increasing gradually to greatest diameter, very large worms, spermiducal gland looped laterally to bursa .... *Xironogiton occidentalis*

4′ Teeth-bearing margin of jaws sublinear, dental formula 4/4 to 6/6, segments V-VII much broader than terete anterior segments, small worms, spermiducal gland extending entally to opposite body wall .... *Xironogiton kittitasi*

Xironogiton instabilis (Moore)

Figures 1, 2

Branchiobdella instabilia Moore, 1894: 425–427.—Smallwood, 1906: 100–111.—Ellis, 1912: 484.
Bdellodrilus instabilis.—Pierantoni, 1912: 22.—Hall, 1914: 190, 192.
Xironogiton oregonensis oregonensis Ellis, 1919: 249–251.
Xironogiton oregonensis pectinatus Ellis, 1919: 251.
Xironogiton instabilius.—Ellis, 1919: 252–253.
Xironogiton instabilius instabilius Goodnight, 1940: 45–47.—Holt 1949:536.—McManus, 1960: 421–427.
Xironogiton instabilius oregonensis.—Goodnight, 1940:47–48.
Xironogiton instabilius.—Berry and Holt, 1959: 5–11.—Hobbs, Holt and Walton, 1967: 64.—Holt, 1968a: 82–84, 86, 88, 91; 1969: 194, 196–197, 201–202, 213.
Xironogiton instabilia.—Franzén, 1962: 369–383.

Type-specimens.—The material from Watauga County, **North Carolina,** and Delaware County, **Pennsylvania,** upon which Moore (1894: 425) based *Branchiobdella instabilia,* has not been found in Moore's collections, now at the National Museum of Natural History (Marvin Meyer, personal communication), and is presumed to have been lost. (Much of Moore's extensive collections were destroyed by vandals while he was living at Media, Pennsylvania). There is no dispute as to the identity of the eastern populations of the species.

Diagnosis.—Medium sized branchiobdellids (length about 2.0–2.7 mm); segments I–IV terete, segments V–VIII broadly flattened, often indistinguishable externally; jaws subrectangular, dental formulae from about 4/4 to 11/11, teeth often, but not always of unequal length; bursa subspherical to pyriform; spermiducal gland extending dorsad, bending mesad over bursa never extending to opposite body wall; spermatheca clavate, very small.

Etymological note.—The correct form of the name of this species is that used by Pierantoni (1912: 22). The Latin word "*instabilius*" is a neuter comparative meaning "more unstable: "*instabilia*" is a neuter *plural* in Latin and is, therefore, impossible as a modifier of any singular noun, while "*instabilis*" means "unstable" and is either masculine or feminine in form. Since the word, in all the forms in which it has been used, is clearly intended as an adjective in the nominative singular, it must, then, be written as "*instabilis*" instead of the impossible "*instabilia*" or the awkward, at least, "*instabilius*" first used by Ellis. Again, I am indebted to Dr. MacAdoo who furnished me with the information on which this nomenclatural decision is based.

Description.—Individuals of *Xironogiton instabilis* (Figure 2a) are worms of medium size. The average length of ten mature specimens selected at random from throughout the range of the species is 2.3 mm (2.0–2.7 mm); the greatest width, 1.1 mm (0.8–1.3 mm). The head is somewhat longer than wide, but not greatly so, a little less in diameter than the sucker and only slightly shorter than the combined length of the first four, terete, trunk segments. The peristomium is divided by shallow lateral incisions into upper and lower lips, each with shallow median indentations, and is set off by a sulcus from the remainder of the head which shows no other external signs of segmentation.

Segments V through VIII are depressed and form, in effect, a large sucker that encloses the true sucker, except for the latter's posterior-most part. Segments X and XI are incorporated into the structure of the sucker. The expansion of the flattened segments is accomplished by dorsoventrally oriented muscles of the septa (*cf.* Ellis's "buttress-like supports"; Ellis, 1919: 243). The edges of the expanded segments are generously supplied with groups of unicellular glands that appear in hematoxylin-eosin stained section to be of the same nature as those found throughout the epidermis of all branchiobdellids, indeed the lateral-most part of the flattened segments is simply an extension of the epidermis.

The mouth is surrounded internally by about twelve oral papillae which are not easily seen except with the aid of the higher powers of the microscope in favorably arranged specimens. The "pharyngeal diverticula", thought by Elis (1919: 243, 247) to be of diagnostic value, are not diverticula at all, but sulci (expansions) of the lumen of the pharynx that may correspond to the segmentation of the head. There may be three such pharyngeal sulci in *X. instabilis* (they are difficult to see in some specimens).

The jaws (Figure 2d, e) are as described by Ellis (1919: 252–253), but the variation in number and arrangement of the teeth are greater than he observed; ranging from 3/4 to 11/11, but there is no detectable geographical pattern to these differences in number of teeth. Both jaws usually have the same number of teeth.

Ellis (1919: 247) stressed, in his generic diagnosis, that the "alimentary canal [is] looped once or twice in segment VII. . . ." This is not so in *X. instabilis.* The gut is expanded intrasegmentally in almost all branchiobdellids and these expansions are exagerated by the flattening of the trunk in *X. instabilis,* although, as Ellis noted, the gut is pushed to one side and reduced in diameter in segment VI by the enlarged male reproductive organs.

The reproductive systems of *X. instabilis* have been described in some detail (Holt, 1949: 538–550) and the account of them that follows, with some changes in terminology, is a condensation of that report.

The spermiducal gland is long: its ental "blind" end lies dorsally above the bursa near the mid-line of the animal, courses laterad ectally along the dorsal border of the bursa and runs ventrad along the lateral end of the latter to its junction with the ejaculatory duct. Its ental third is composed of glandular cells that stain lightly and contain basophilic granules; the median third is composed of cells packed with coarser, eosin staining granules; while the ectal third is similar to the ental portion. The vasa deferentia enter the spermiducal gland near the junction of its ectal and median portions.

The ejaculatory duct is a long, slender muscular tube that runs mesad and then dorsad between the spermiducal gland and the bursa to its junction with the ental apex of the latter.

Together with the spermiducal gland, the bursa fills from 1/2 to 3/4 of the body cavity of segment VI. The bursa is divided into the usual penial sheath and atrium separated incompletely by an inwardly directed atrial fold. The penial sheath region is remarkable by virtue of its extremely thick muscular wall (Holt, 1949: pl. 3, fig. 21) which encloses almost completely the cone-like and likewise heavily muscular penis: the latter the ectal end of the ejaculatory duct. Ellis (1919: 250) described the bursa of *X. o. oregonenis* and *X. o. pectinatus* as small and spherical. I concurred in this description in my unpublished dissertation (Holt, 1951: 199). Through the courtesy of Dr. Marian H. Pettibone I have had the opportunity to examine, not only the types, but the entire type series of both these nominal subspecies. Both Ellis and I were wrong. The animals are small and submature, but the bursae of all in which the reproductive organs can be seen (some worms are mounted in what appears to be Hoyer's medium and are worthless; the notation "co-type" on some of the slides is in a handwriting other than that of either Ellis or me) are identical in form and proportional size to those of other members of the species.

The clavate spermatheca is, in comparison to the bursa and spermiducal gland, riduculously small (Figure 2b). The ectal duct widens gradually into the bulbular portion which, however, contains spermatozoa within its narrow lumen. [Again, the spermatheca has been incorrectly described. It does not have an ental process (Holt, 1960: 64) as implied by Ellis (1919: 250) and Holt (1951: 199), but is, in the type series referred to above, as described herein and previously (Holt, 1949: 547–549)]. The presence of spermatozoa in the spermathecal bulb is significant in view of the presence of packets of spermatozoa found on the dorsal surface of a number of specimens (Holt, 1949: 549), suggesting the possibility of a leech-like "hypodermic" impregnation, but such sperm packets have been seen rarely since and never on specimens of other members of the genus with similarly small spermathecae. The whole question of the reproductive processes, in not only *X. instabilis,* but also its congeners, needs investigation.

Variation.—*Xironogiton instabilis* varies in the number of teeth and the order of short and long ones on the jaws. But these variations present no consistent pattern and Ellis's (1919: 241–243) attempt to develop a formula for the arrangement of large and short teeth fails. In some specimens, the intersegmental furrows separating the posterior segments are obscure. Otherwise there are the common age associated variations in size (within species specific limits) and shape and position of internal organs attributed to variations in killing agents used and the animals position at death.

Hosts.—*Xironogiton instabilis* has been found associated with the following hosts (and can be expected to occur on many others within its range): *Cambarus b. bartonii* (Fabr.), *C. (Jugicambarus) carolinus* (Erichson), *C. (Hiaticambarus) longulus* Girard, *C. (H.) longirostris* Faxon, *C. (Puncticambarus) acuminatus* Faxon, C. (P.) *veteranus* Faxon, *Orconectes erichsonianus* (Faxon), *O. immunis* (Hagen), *O. limosus* (Rafinesque), *O. obscurus* (Hagen), *O. p. propinquus* (Girard), *O. transfuga* Fitzpatrick, *Pacifastacus g. gambelii* (Girard), *P. leniusculus leniusculus* (Dana), *P. l. klamathensis* (Stimpson), *P. l. trowbridgii* (Stimpson).

Distribution.—In the western part of the continent, *X. instabilis* is known from Sonoma and Tuolumne Counties in California, through Oregon and Washington to Clallam County at the northern tip of the Olympic Peninsula, and eastward into Idaho and Lincoln County, Wyoming. In the east, the species ranges from northern New York southward to the mountains of North Carolina and Tennessee with its westernmost known limit at Natural Bridge State Park in Powell County, Kentucky. The species may be expected to occur in Canada, where little collecting has been done, in both the east and west. The apparent significance of this extremely disjunct distribution has been discussed above in the section on "Evolutionary and Zoögeographical considerations."

Material examined.—Thousands of specimens from at least 194 collections, including topotypical material from Watauga County, North Carolina, USNM 36783 (PCH 138) (see mimeographed "Locality Data for the Specimens of the genus *Xironogiton*" referred to above).

Remarks.—Little is known of the ecology of the branchiobdellids (Holt, 1968a), but a few things are known of the habits and habitats of *X. instabilis*. The species is confined to cold mountain streams in the east, at least in the southern part of its range, and all the streams from which it has been taken in the west are of the same character, although they reach the hightide level on the coast. It is known (Berry and Holt, 1959) that the species is intolerant of warm waters. Brown (1961) confirmed my field observations that it is essentialy confined to the chelipeds of the hosts.

The history of the names given the species has been reviewed above from a legalistic standpoint, but the decision to reduce a nominal species to synonomy is a biological one and in this case deserves a few remarks. It is not clear from his descrption of *X. oregonensis* why Ellis (1919: 249–251) separated the twenty-two specimens he studied from Moore's (1894) *"instabilia"*, but it is likely that it was done on the basis of a presumed difference in the number of teeth borne on each jaw and the subtle influence of geography. Goodnight (1940: 48), on the basis of the overlap in dental formulae that he observed, reduced *oregonensis* (including both *X. o. oregonensis* and *X. o. pectinatus*) to the rank of a western subspecies of "*instabilius*". Apparently he did not perceive that this overlap includes without remainder the eastern populations as well. Believing that Goodnight was mistaken I made, several years ago, an extensive analysis of the dental formulae of western and eastern populations and convinced myself that not only is it impossible to separate the western populations into two taxa; furthermore on the basis of a careful comparison of size, segmentation, proportions of reproductive organs and other possible characters, I became convinced that the eastern and western populations are anatomically indistinguishable.

Xironogiton occidentalis Ellis

Figure 1, 3

Xironogiton occidentalis Ellis, 1919: 248–249.—Goodnight, 1940: 44–45

Type-specimens.—USNM 17639, Crab Creek, **Washington,** taken from *Astacus klamathensis* Stimpson by John T. Nichols, U.S. Bureau of Fisheries (Ellis 1919: 248). Date unknown.

Diagnosis.—Large branchiobdellids (length about 4.5–7.5 mm); body flattened, gradually widening from segment I to segment VII, segments I–VII usually distinguishable externally; jaws subrectangular, teeth of varying length, dental formula 6/6; bursa subglobose, heavily muscular; spermiducal gland inverted U-shaped, middle portion reaching dorsal body wall; spermatheca calvate, small, thick-walled.

Description.—*Xironogiton occidentalis* is a very large branchiobdellid and is immediately recognizable on the basis of body shape and its size that is not exceeded by any member of the order known to me. The holotype is 4.5 mm in length and the paratype 5.0 mm (Ellis, 1919: 249). The dimensions of five mature worms from Lincoln County, Oregon, are as follows: *total length,* 6.6 mm (5.4–7.5 mm); *greatest diameter*, 2.1 mm (2.0–2.1 mm); *head length*, 1.5 mm (1.1–1.7 mm); *head diameter*, 1.1 mm (0.95–1.3 mm); *diameter*, *segment I*, 1.1 mm (0.95–1.1 mm); *diameter*, *sucker* 1.3 mm (1.1–1.5 mm). Specimens from Washington that I have seen are of comparable size. Though the worms I have studied are larger than Ellis' types, there is no doubt about their identification.

The head is large and muscular and has no external sulci except the prominent one that sets off the peristomium. The latter is, as usual, composed of upper and lower lips; the upper is entire, but the lower has a shallow median emargination. An indeterminate number of obscure oral papillae are present and one prominent pharyngeal sulcus at the midlength of the pharynx, though less apparent ones may be present just behind the jaws and posteriorly at the posterior border of the head.

The head and the first two or three segments are terete, but the trunk flattens and widens gradually posteriorly in such a way that the posterior end is rounded and the sucker is not readily detectable in

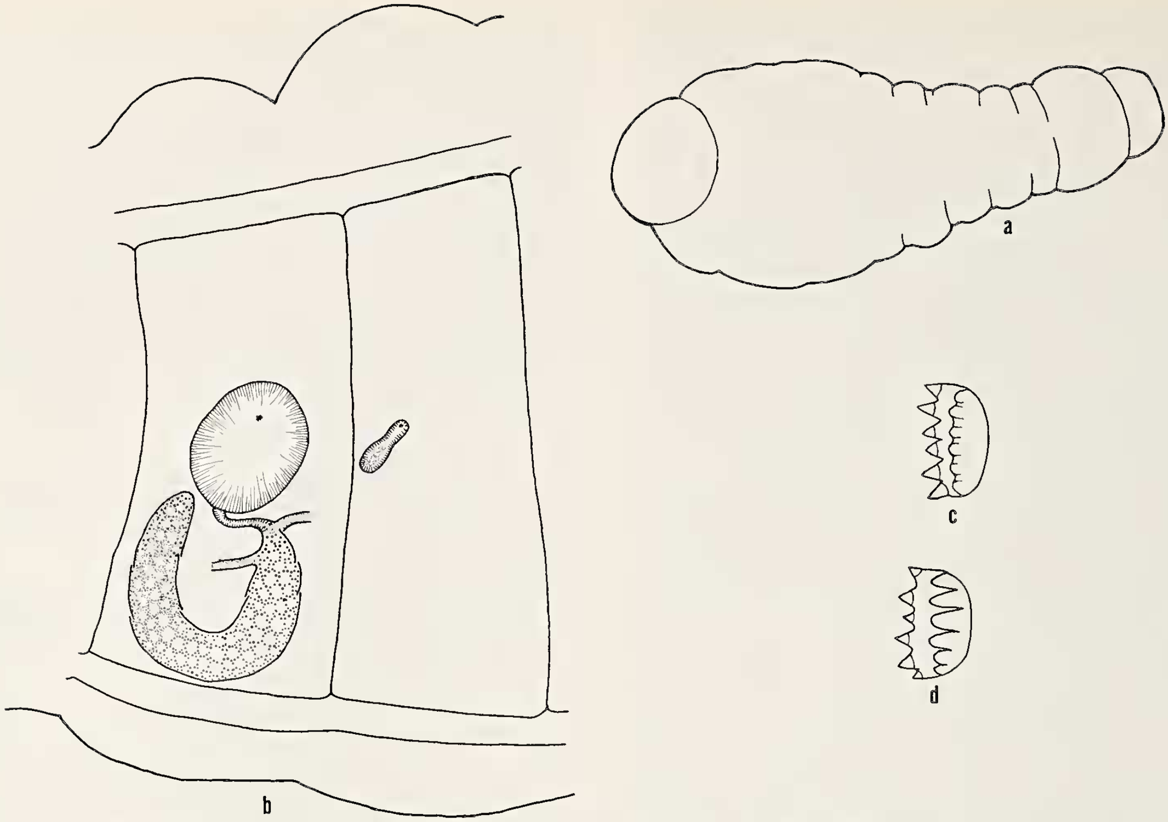

FIG. 3—*Xironogiton occidentalis*. a, ventral view of entire animal from Lincoln County, Oregon; b, ventral view of reproductive systems; c, upper jaw; d, lower jaw. (c and d from Ellis, 1919: 249).

dorsal view. The margins of the posterior segments are not greatly expanded and the obvious flattening of them is more apparent than real, as a study of serial sections reveal, and they contain muscle fibers that are thinner than those of the body wall and the glandular elements are hardly more numerous than in other parts of the epidermis. The "adhesive glandular disks" (Ellis, 1919: 243) are simply not there and Ellis must have been referring to the lateral expansions of the epidermis in this region.

The jaws are well described by Ellis and I have used his illustrations of them (Figure 3c, d). The dental formula is 6/6 and the body of the jaws is composed of prominently thickened ridges which terminate in the teeth and are held together by thinner portions of the presumably chitinous structure.

Again, the gut does not form an "S"-shaped curve in segment VII (Ellis, 1919: 249) and, in actuality, is unremarkable were it not for the size of the animals and a correspondingly more readily apparent expansion of the gut in each segment.

Except for stating "spermatheca simple; testes present in segments V and VI joining the atrium in segment VI; a long accessory sperm tube present; . . .'.' Ellis (1919: 249) had nothing to say about the reproductive systems of *X. occidentalis*. A fuller account is called for.

The "accessory sperm tube" is the structure I have called the "prostate" in other genera, *e.g.*, *Cambarincola*, but in some cases Ellis (1919) and Goodnight (1940) used the term for the structure I refer to as the "spermiducal gland" (see Holt, 1960, for a fuller discussion of anatomical nomenclature in the branchiobdellids).

In *X. occidentalis*, the spermiducal gland begins entally in the posterior lateroventral region of the coelom of segment VI, runs dorsad to the dorsal border of the coelom, bends there to course ventrad to the ventral body wall where it narrows and becomes muscular to form the ejaculatory duct. The anterior vas deferens, formed by the union of the vasa efferentia of segment V enters at the juncture of the spermiducal gland and the ejaculatory duct, the posterior one enters the gland a short distance entally. The ectal and ental portions of the spermiducal gland stain darkly with hematoxylin; the middle portion is composed of lighter staining and more vacuolated cells.

The ejaculatory duct is a thin muscular tube that loops its way dorsad to the dorsal extrtmity of the bursa which it enters there to form the muscular penis which is hardly distinct from the heavily muscular wall of the penial sheath. The atrial fold of the bursa is formed by the projection into the bursal lumen of the penial sheath. The bursal atrium is enclosed by a thin wall which consists of hardly more than the investing peritoneum and a very thin sheet of muscle fibers.

The spermatheca is very small with a proportionally thick muscular wall throughout its extent, so that there is no sharp boundary between ectal duct and bulbular regions, though a mass of spermatozoa is always found in its slightly expanded inner portion.

Variation.—Other than a rather unusual range in size of mature individuals (those with spermatozoa filling the testicular segments) no differences of note were observed.

Hosts.—*Xironogiton occidentalis* has been found associated with the following crayfish hosts: *Pacifastacus l. leniusculus* (Dana) *P. l. klamathensis* (Stimpson), and (Goodnight's records, 1940: 45) *P. l. trowbridgii* (Stimpson), and *P. g. gambelii* (Girard).

Distribution.—Crab Creek, the type-locality of *X. occidentalis,* arises west of Spokane, Washington, and following a westward course through the arid region of the central part of the state, flows into the Columbia River. I, however, have taken specimens of *X. occidentalis* only in streams of the western slope of the Coastal Range which flow directly into the Pacific Ocean. Goodnight (1940: 45), whose records of this species can be accepted, since its size and shape is distinctive, records it from Harney County, Oregon, a region of central Oregon that must be much like the type-locality; Vernonia, Oregon, again in the Coastal Range and near some of my localities; and Young River, Oregon, which I have been unable to locate. All this suggests that *X. occidentalis* may have a relatively widespread, but discontinuous, distribution in the Columbia (including the lower Snake) River drainage and in the streams of the Coastal Range that flow directly into the Pacific in Washington and Oregon (? British Columbia).

Material examined.—Twenty specimens from the following localities: **Oregon,** Lincoln County, Slick Rock Creek, 5 miles southwest of Rose Lodge on state highway 18, taken on *Pacifastacus l. leniusculus* by P. C. & V. F. Holt, July 13, 1960 (USNM 48564; PCH 1122: 7 specimens). **Washington,** Clallam County, Mill Creek at Forks on U.S. Highway 101, taken on *Pacifastacus leniusculus trowbridgii* (Stimpson) by P. C. & V. F. Holt, July 16, 1960 (USNM 48567; PCH 1137: 5 specimens); Gray's Harbor County, West Fork Hoquiam River at crossing of U.S. Highway 101, 14.5 miles south of Humptulips, taken on *P. l. klamathensis* by P. C. & V. F. Holt, July 16, 1960 (USNM 48566; PCH 1132: 2 immature specimens); Wahkiakum County, Gray's River, 21 miles east of Gray's River on U.S. Highway 830, taken on *P. l. klamathensis* by P. C. & V. F. Holt, July 14, 1960 (USNM 48565; PCH 1130: 6 specimens).

Remarks.—It is known (Brown 1961; personal field observations) that most species of *Xironogiton* are essentially confined to the distal portion of the chelipeds of their hosts. This, relying on my memory of twelve years ago, is not true of *X. occidentalis* and, indeed, the very size of animals of this species argues against them occupying such a microhabitat. Rather, they occur on the dorsal surface of the carapace, and perhaps elsewhere, of their hosts. The size of the animals is remarkable and, as in the case of *Cambarincola ingens* Hoffman, seems to be due to an increase in the size of individual cells, especially the muscle cells of the body wall, which raises the interesting possibility of the existence of polyploidy among the branchiobdellids.

Xironogiton fordi, new species

Figures 1, 4

Type-specimens. Holotype and two paratypes, USNM 48549: three paratypes, USNM 48550; two paratypes, PCH 785, taken on *Pacifastacus gambelii connectens* (Faxon) from Riley Creek at Idaho Fish Hatchery, Gooding County, **Idaho** by P. C. and V. F. Holt, Judson and Willia Ford, July 14, 1958.

Diagnosis.—Small branchiobdellids (length about 1.6 to 2.1 mm); segments I–IV terete, segments V–VIII broadly flattened, segments, V–VII hardly or not at all distinguishable externally; jaws subrectangular, anteroposterior dimensions much less than transverse ones, teeth always subequal in length, dental formula from 6/6 to 11/11; bursa ellipsoid; spermiducal gland arising ectally at ventral border of coelom, curving dorsally over bursa to about midline of body or beyond; spermatheca clavate, directed laterad, thick-walled, 1/4 or more width of segment V in length.

Etymology.—This species is named in honor of the late Judson Ford whose hospitality and guidance while collecting branchiobdellids in southern Idaho were sources of great help and comfort to me.

Description.—Members of the species *Xironogiton fordi* are small-to-medium-sized worms. The holotype has the following dimensions: *total length,* 2.1 mm; *greatest diameter,* 0.9 mm; *head length,* 0.5 mm; *head diameter,* 0.4 mm; *diameter, segment I,* 0.3 mm; *diameter, sucker,* 0.5 mm. The holotype and four paratypes have the following average dimensions: *total length,* 1.9 mm ,1.6–2.1 mm);*greatest diameter,* 0.9 mm (0.6–1.0 mm); *head length,* 0.5 mm (0.4–0.5 mm); *head diameter,* 0.4 mm (0.3–0.4 mm); *diameter, segment I,* 0.3 mm (0.6–0.4 mm); *diameter, sucker,* 0.4 mm (0.3–0.5 mm).

The head is almost as great in diameter as its length; it has no external sulci except the peristomial one. The peristomium is hardly, if at all, divided into upper and lower lips and there are no median emarginations of the lips. Oral papillae are present. Internally, the pharynx is expanded in the type series and pharyngeal sulci are obscure: serial sections reveal two.

The jaws are distinctive. Subrectangular, as are all those of the genus, the teeth-bearing border is straight, the teeth are of equal length, ranging in number for each jaw of an individual from six to eleven; the number of teeth is the same for both jaws of a single specimen.

The first four segments are terete, increasing only slightly in diameter through segment IV. The remaining segments are dramatically flattened, much broader, and intrasegmental furrows 5/6 and 6/7 are obliterated. Segment VIII is set off by furrow 7/8; the remaining segments (IX–XI) are incorporated into the sucker.

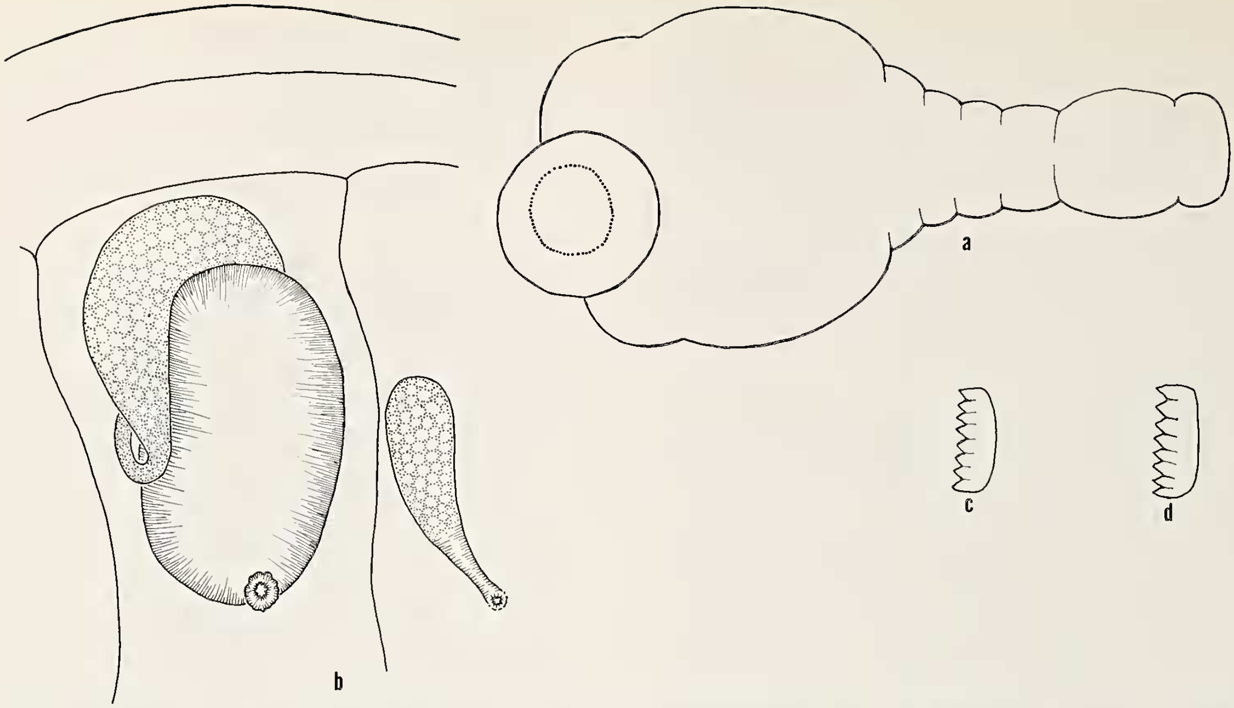

FIG. 4—*Xironogiton fordi.* a, ventral view of holotype; b, ventral view of reproductive systems of holotype; c, lower jaw of holotype, d, upper jaw of holotype.

The gut is not "looped" in any segment, but is displaced to the left side of the coelom in segment VI.

The spermiducal gland entally extends to the dorsomedian border of the bursa, curves ventrad along the lateral margin of the latter, narrowing rapidly as it approaches its junction with the ejaculatory duct. The vasa deferentia enter it immediately before its narrowed ectal part becomes the ejaculatory duct. The gland is histologically different along its length; the ental and ectal parts taking a darker stain with hematoxylin than the lightly staining median portion.

The ejaculatory duct is a thin muscular tube that runs along the lateroposterior border of the bursa to enter the latter at its lateroposterior apex where it forms a heavily muscular penis which projects through the bursal atrium to the ventral wall of the bursa. Heavily muscular atrial folds are present and the atrial wall itself is thick. In shape, the bursa is an almost perfect ellipsoid in longitudinal section.

The spermatheca, through typical of the genus in shape (clavate) and in its thick muscular wall, extends entally posterolaterad and is relatively large, reaching a length of about 1/4 the width of segment V. There is no definite boundary between ectal duct and bulb and the bulb always contains spermatozoa in mature specimens.

Variation.—The variation in number of teeth is noted above and I have deliberated gravely as to whether to include the worms from northwestern Wyoming, where the specimens with the largest number of teeth are found, in the species. But variability in the number of teeth occurs in other species of the genus. One serially sectioned animal from Lincoln County, Wyoming, shows the reverse of the staining properties of the spermiducal gland from those described for a sectioned and stained specimen of the type series. In spite of the apparent constancy of the staining properties of the spermiducal gland in *X. instabilis,* too little is known of the physiological functions of the glands associated with the male reproductive system of any branchiobdellid to allow one to draw any conclusions from this variation, which well may simply represent a different stage in the secretory cycle of the gland. The coherence and constancy of the other observable characters of the specimens studied convinces me of their conspecificity.

Affinities.—*Xironogiton fordi* is indistinguishable in size and body proportions from *X. instabilis,* except for the easily overlooked median emarginations of the lips of the latter. The jaws and teeth of *X. fordi* are diagnostic: the narrow linear jaws and teeth of equal length are found in no other species of the genus. The ellipsoid bursa differs in shape from the pyriform (often deformed and elongated in the transverse plane of its segment) one of *X. instabilis* and the spermathetca is distinctly larger in *X. fordi,* proportionately the largest in the genus.

The large size of *X. occidentalis* greatly exceeds that of *X. fordi* and the other species of the genus. The bursa of these two species differ in shape and proportional size: that of *X. occidentalis* is subspherical and it is proportionately smaller. The spermatheca of *X. fordi* extends, dorsal to the bursa, entally to approximately the mid-line of the body; that of *X. occidentalis* forms an inverted "U" lateral to the bursa.

Distribution.—The Snake River and its tributaries in Idaho and Wyoming and, presumably (I have not been able to accurately place the Lincoln County locality), the Bear River drainage — part of the Great Basin drainage with no outlet to the sea now, but formerly a part of the Snake River system. The alternative would put this record in the Colorado River drainage by way of the Green River and this is unlikely since the host crayfish do not inhabit the Colorado system. The other two localities on the Absaroka Plateau (at an elevation of approximately 7,800 feet) in Wyoming may represent altitudinal records for any branchiobdellid.

Hosts.—*P. g. gambelii* and *P. g. connectens.*

Material examined.—Thirty-three specimens: the type-series and 3 others (PCH 785: 11 specimens); **Wyoming,** Lincoln County, Crow Creek, taken on *Pacifastacus g. gambelii* by Tracey (first name unknown), September 28, 1946, USNM 48557 (PCH 420: 10 specimens); Teton County, Polecat Creek, taken on *P. g. gambelii* by Lipke B. Holthuis, July 29, 1960, USNM 48553 (PCH 1327: 6 specimens); Yellowstone National Park, Crayfish Creek at Moose Falls, taken on *P. g. gambelii* by Robert C. Powell, 1961, USNM 48554 (PCH 1501: 6 specimens).

Xironogiton cassiensis, new species

Figures 1, 5

Type-specimens.—Holotype, USNM 48555 and nine paratypes, USNM 48556; seven paratypes, PCH 782, taken on *Pacifastacus g. gambelii* from the Raft River between Alma and Bridge on county road, Cassia County, **Idaho,** by P. C. and V. F. Holt and Ray Bronson, July 13, 1958.

Diagnosis.—Small branchiobdellids (length about 1.5 to 2.1 mm); segments I–IV terete, segments V–VIII broadly flattened, distinct externally; jaws subrectangular, tooth bearing margin concave, lateral teeth longer than median ones, dental formula 6/6 to 7/7; bursa ovoid; spermiducal gland long, extending entally well beyond dorsomedian margin of bursa; spermatheca small, thick-walled, directed posteriorad.

Etymology.—For Cassia County, Idaho, the type locality.

Description.—Individuals of *Xironogiton cassiensis* are small members of the genus: only *X. kittitasi* is as small. The holotype has the following dimensions: *total length,* 2.1 mm; *greatest diameter,* 0.8 mm; *head length,* 0.4 mm; *head diameter,* 0.3 mm; *diameter, segment I,* 0.3 mm; diameter, sucker, 0.4 mm. The holotype and four randomly selected paratypes have the following average dimensions: *total length,* 1.8 mm (1.5–2.1 mm); *greatest diameter,* 0.7 mm (0.6–0.8 mm); *head length,* 0.4 mm (0.3–0.4 mm); *head diameter,* 0.3 mm (0.3–0.3 mm); *diameter, segment I,* 0.3 mm (0.3–0.3 mm); *diameter, sucker,* 0.3 mm (0.3–0.4 mm).

Segments I–IV are terete, increasing gradually in diameter posteriorly so that the flattened posterior segments are not sharply demarcated in transverse diameter from the anterior ones. The head, except for the peristomial sulcus, has no external signs of segmentation. The peristomium is not obviously divided into upper and lower lips, except that its dorsal part projects beyond the lower. Rarely the lower "lip" shows a faint median emargination and in some specimens it clearly bears at its inner border a number (not easily determined) of oral papillae. In other specimens, these are not detectable and they are apparently entirely absent from one serially sectioned paratype. Internally, three pharyngeal sulci are evident.

The jaws have a concave tooth bearing border; the median teeth are always shorter than the lateral ones; the dental formula is 6/6 or 7/7.

The gut is, indeed, looped in segment VIII; a feature regarded by Ellis (1919: 247) as a generic character. This has been referred to above and it is strange to find that this peculiarity of the gut occurs only in a species of the genus of which Ellis almost surely never saw a specimen on the basis of his locality records.

The spermiducal gland is very long: its ental portion extends dorsal to the bursa almost to the body wall opposite to the half of the segment that is filled with the major portions of the male reproductive system. The division of the gland into distinct histologically different regions is not evident in serial sections, although some more heavily granular cells, which stain deeply with eosin, are intermingled with, along the median portion of the gland, those not so granular, that are stained predominantly with hematoxylin. The anterior vas deferens enters the gland at its junction with the ejaculatory duct; the posterior at a point approximately level with the laterodorsal margin of the bursa.

The ejaculatory duct is a slender tube which meanders dorsad along the lateral side of the bursa to enter the latter at its apex opposite its external opening. The bursa, itself, is distinguished by its quite symmetrical ovoid shape; its internal structure conforms to that of most other members of the genus. As is generally true of the species of *Xironogiton,* the bursa and spermiducal gland fill half of the coelom of segment VI.

The clavate spermatheca is short, thick-walled, with ectal duct and bulb poorly demacated (though spermatozoa are always present in the fundus) and directed posteriorad underneath the gut.

Variation.—The variability in tooth number has been noted and it occurs within a single population from Lincoln County, Wyoming. It is not, therefore of any taxonomic significance. More significantly, these four specimens and one from Lake County, Idaho, have shorter spermiducal glands that end entally at about the mid-line of the body. It is with extreme reluctance that I assign these specimens, from the Great Salt Lake drainage, to *X. cassiensis* and I would not do so except for the conformity in jaw structure and, more importantly, the fact that I have a single specimen from Gooding County, Idaho, with a 6/6 dental formula and a spermiducal gland of intermediate length. Future collecting quite likely will demonstrate the specific distinctness of the Great Salt Lake Basin (Bear River drainage) specimens. It might be noted, though, that the latter occur on the same host as the type-series.

Affinities.—*Xironogiton cassiensis* has the body

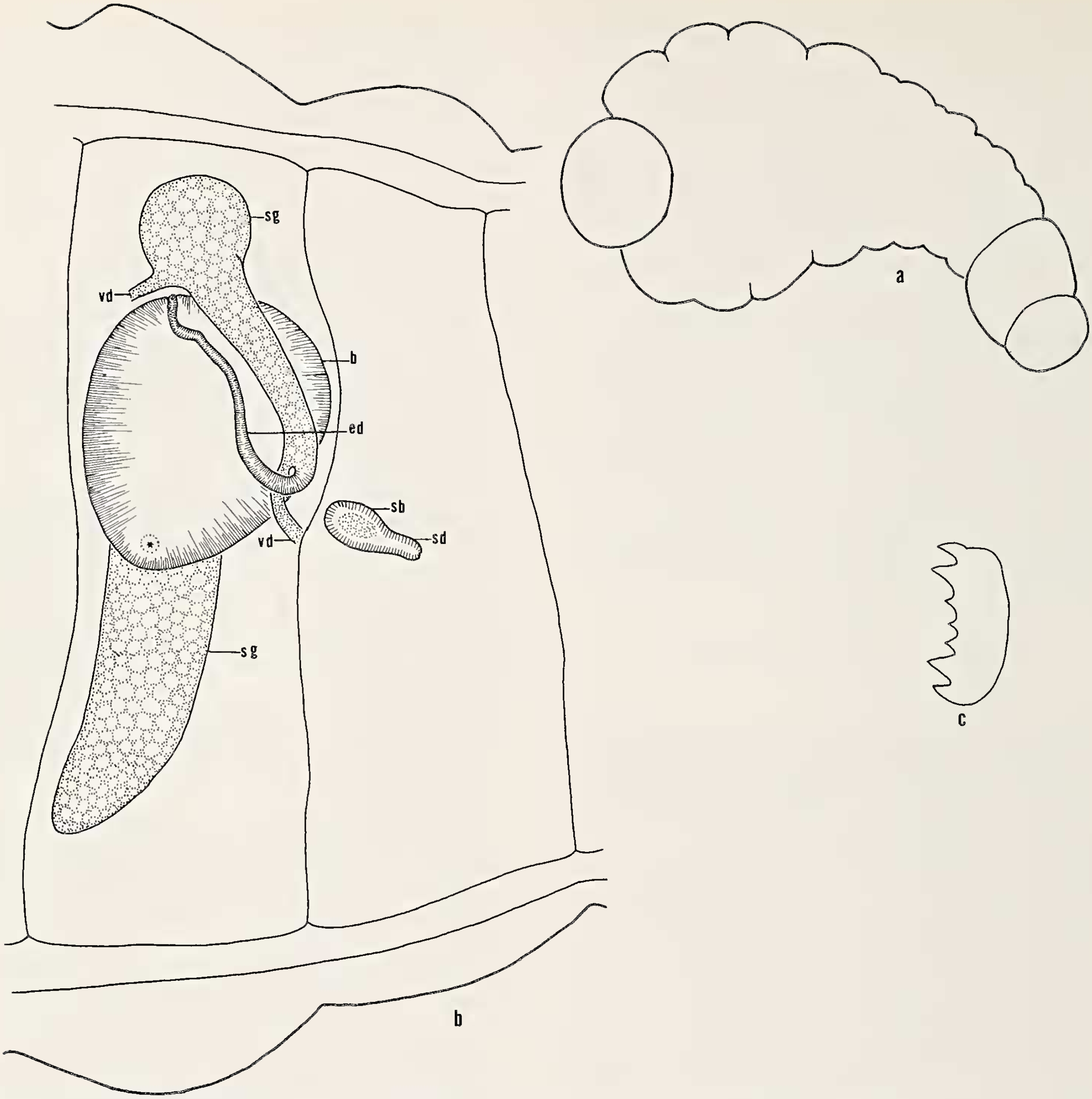

FIG. 5—*Xironogiton cassiensis*. a, ventral view of holotype; b, ventral view of reproductive systems of holotype; c, jaw of paratype. (Abbreviations: *b* = bursa; *ed* = ejaculatory duct; *sb* = bulb of spermatheca; *sd* = ectal duct of spermatheca; *sg* = spermiducal gland; *vd* = vas deferens).

form of *X. occidentalis*, but differs from the later in the shape of the jaws, a concave teeth-bearing margin in the former and a convex one in the latter. The bursa of *X. cassiensis* is distinctly egg-shaped and differs in this respect from the other species of the genus. The distance between the junctions of the vasa deferentia with the spermiducal gland is greater than in the other species, but resembles *X. occidentalis* most closely in this respect. The spermiducal gland differs from that of *X. instabilis*, *X. fordi* and *X. occidentalis* in its greater proportional length, which, however, does not reach that of *X. kittitasi*. In addition, it appears to be unique in not being divided into histologically distinct portions (but, *cf. X. kittitasi* below). The bulbular wall of the spermatheca is thicker than in other species of the genus.

Hosts.—*Pacifastacus g. gambelii, P. g. connectens.*

Distribution.—The middle of Snake River drainage in Cassia (Raft River) and Gooding Counties, Idaho, and the Bear River drainage in Lincoln County, Wyoming, and Lake County, Idaho.

Material examined.—Twenty-three specimens: the type-series (PCH 782: 17 specimens); **Idaho,** Lake County, Paris, taken on *Pacifastacus g. gambelii* by C. L. Hayward and D. Eldon Beck, October 28, 1950, USNM 48558 (PCH 424: 1 specimen); Gooding County, Riley Creek (Idaho Fish Hatchery), taken on *P. g. connectens* by P. C. and V. F.

Holt, and J. and W. Ford, July 14, 1958, USNM 48559 (PCH 785: 1 specimen); **Wyoming,** Lincoln County, Crow Creek, taken on *P. g. gambelii* by Tracey (first name unknown), September 28, 1946, USNM 48557 (PCH 420: 4 specimens).

Xironogiton kittitasi, new species

Figures 1, 6

Type-specimens.—Holotype, USNM 48560, two paratypes, USNM 48561; two paratypes, PCH 1141, taken on *Pacifastacus leniusculus klamathensis* (Stimpson) from Teenaway River, Kittitas County, **Washington,** by P. C. and V. F. Holt, July 18, 1960.

Diagnosis.—Small (length about 1.4 to 2.0 mm); segments I–IV terete; segments V–VIII broadly flattened, hardly or not at all distinguishable externally; jaws subrectangular, median teeth always shorter than lateral ones, dental formula 4/4 to 6/6; bursa irregularly ellipsoid; spermiducal gland very long, extending from ectal end dorsad to dorsal body wall, thence transversely to opposite laterodorsal body wall, exceeding in length total transverse diameter of segment VI, ectally narrowing gradually to junction with ejaculatory duct, vasa deferentia entering at different levels of narrowed ectal portion; spermatheca small, clavate, directed laterad.

Etymology.—Genitive form of Kittitas, the county in Washington which contains the type-locality.

Description.—*Xironogiton kittitasi* includes the smallest known members of the genus. The holotype has the following dimensions: *total length,* 1.5 mm; *greatest diameter,* 0.8 mm; *head length,* 0.3 mm; *head diameter,* 0.25 mm; *diameter, segment I,* 0.2 mm; *diameter, sucker,* 0.3 mm. The type-series (five specimens) have the following average dimensions: *total length,* 1.6 mm (1.4–2.0 mm); *greatest diameter,* 0.8 mm (0.6–0.9 mm); *head length,* 0.3 mm (0.3–0.4 mm); *head diameter,* 0.3 mm (0.25–0.35 mm); *diameter, segment I,* 0.2 mm (0.2–0.3 mm); *diameter, sucker,* 0.3 mm (0.3–0.4 mm).

The head is only slightly greater in length than diameter and has no external sulci except the peristomial one. The peristomium is entire, not divided into upper and lower lips, although it has very shallow, almost indetectable dorsal and ventral indentations. Oral papillae are present. Internally, there are three, not very distinct, pharyngeal sulci.

The teeth bearing margins of the jaws are sublinear; the dental formula varies from 4/4 to 6/6; the median tooth or teeth are invariably shorter than the lateral ones, though the most lateral tooth is not always the longest.

The first two segments are subequal in diameter, the third slightly greater, while segment IV, though noticeably greater in diameter than the first three, is distinctly less so than the broadly flattened posterior segments. Intersegmental furrows between segments V–VIII may or may not be externally evident. The sucker is somewhat greater in diameter than either the head or the somewhat narrower segment I.

The gut may be pushed aside in segment VII by maturing eggs (as it always is by the male organs

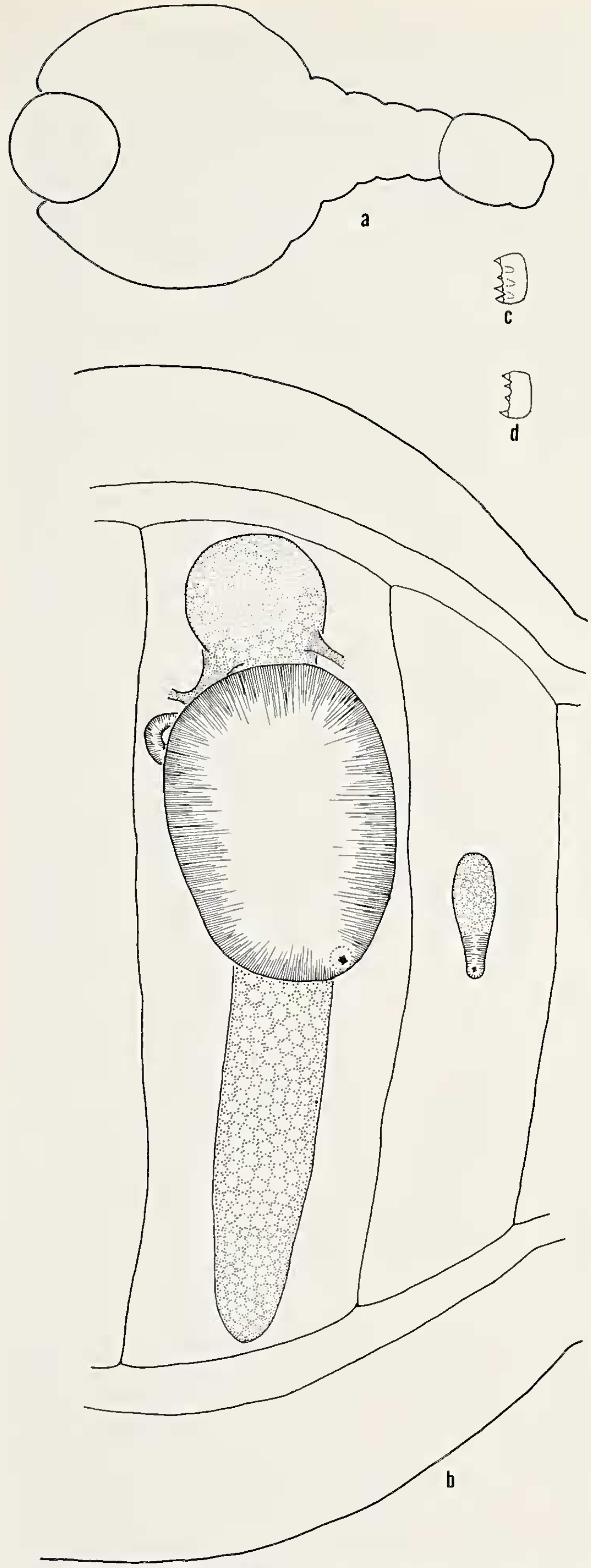

FIG. 6—*Xironogiton kittitasi*—a, ventral view of holotype; b, reproductive system of holotype; c, upper jaw of holotype; d, lower jaw of holotype.

among members of the genus in segment VI) but it cannot truly be said to be "looped".

The spermiducal gland is very long, its "blind" ental end abuts the dorsolateral margin of the body wall and it extends dorsad above the gut and the bursa and then curves ventrad between the bursa and the opposite body wall to the lateroventral margin of the coelom to pass into the muscular ejaculatory duct. It is difficult to determine in my unstained material, that is mounted entire, if the spermiducal gland is histologically differentiated along its length, but approximately the second one-fourth of the gland from its ental end appears to be composed of less granular cells than the remainder, though this is uncertain and I cannot determine whether the expected histological distinctness of the ental, median and ectal portions of the gland exists. The gland narrows ectally before it passes into the ejaculatory duct. The posterior vas deferens enters at the junction of the gland and the ejaculatory duct; the anterior one enters somewhat entally to this junction. These statements should be checked by reference to serially sectioned animals. Nonetheless, the spermiducal gland is, by virtue of its length, one of the most distinctive characters of the species.

The ejaculatory duct is, as usual, a long slender muscular tube that courses dorsad around the lateral margin of the bursa to enter the latter at its posterodorsal apex opposite its external opening. The bursa, itself, is irregularly ellipsoid in shape and its muscular walls are disproportionately thick and the broad conical penis, directed ventromesad, essentially fills the atrial space of the bursa, effectively obliterating the atrial folds, so often prominent in other species, not only of *Xironogiton* but in other genera of the order. Much of the total coelomic space of segment VI is filled by these components of the male reproductive system.

The clavate spermatheca is directed laterad and is, though small, proportionately larger than usual.

Variation.—None noted, other than the variability in the number of teeth remarked upon above.

Affinities.—In body form and size (though sometimes somewhat smaller), *X. kittitasi* is indistinguishable from *X. instabilis* and *X. fordi* and the few specimens studied were almost overlooked as ones of *X. instabilis* until the extreme length of the spermiducal gland was noted. The jaws differ subtly from those of *X. instabilis* in their essentially straight, as opposed to convex, teeth-bearing margins and from those of *X. fordi* in the smaller number of teeth and their unequal length. The bursa is essentially indistinguishable from that of the latter species. The spermiducal gland appears to be differentiated into histological regions—since I have no serial sections of *X. kittitasi* this point is uncertain—which is true of the other members of the genus except *X. cassiensis*. It is unique in its extreme length, approached in this respect only by *X. cassiensis* from which it appears to also differ in the distance between the points of entry into it of the vasa deferentia which is much greater in the latter. It is not easy to determine degrees of affinities among these species, each of which is distinct in some respects that can neither be regarded with assurance as primitive or advanced, except for the tentative postulation of the primitive status of *X. occidentalis*.

Host.—*Pacifastacus leniusculus* (Stimpson).

Distribution.—Upper reaches of the Yakima River drainage on the eastern slopes of the Cascade Range in Washington.

Material examined.—Thirteen specimens: the type-series (PCH 1141: 5 specimens); **Washington,** Kittitas County, (?) irrigation ditch, 7.2 miles east of Ellensburg on U. S. Highway 10, taken on *Pacifastacus leniusculus klamathensis* (Stimpson) by P. C. and V. F. Holt, July 18, 1960, USNM 48562 (PCH 1142: 8 specimens).

Note

I have a number of specimens (PCH 1285) taken from *Cambarus carolinus,* a burrowing crayfish and an unlikely host for a species of *Xironogiton,* on the grounds of the Mountain Lake Hotel, Giles County, Virginia, by Kenneth Simonds and Hugo James, August 10, 1960, that are indisputably members of the genus *Xironogiton.* These specimens differ from *X. instabilis,* which is very common in the region, in the peculiar narrowing and elongation of the posterior part of the body, a feature that I would consider of specific value if I were convinced that it is constant and characteristic of a distinct population. Many efforts to obtain additional specimens failed and since these were taken from crayfish that were out of water on a rainy night, I am inclined to attribute their unusual shape to some influence of the conditions under which they were taken and tentatively assign them to *X. instabilis.* Yet, the possibility remains that these animals do represent a new species and future students of the branchiobdellids should be alerted to this.

Literature Cited

Berry, James W. and Perry C. Holt

1959. Reactions of two species of Branchiobdellidae (Oligochaeta) to high temperatures and low oxygen tensions. *Virginia Agricultural Experiment Station, Technical Bulletin,* 141: 1–11.

Brown, George G.

1961. Some Ecological Studies of the Branchiobdellidae found in Sinking Creek, Giles County, Virginia. Unpublished master's thesis. Virginia Polytechnic Institute and State University. 67 pages, figures 1–5.

Ellis, Max M.

1912. A New Discodrilid Worm from Colorado. *Proceedings of the United States National Museum,* 42(1912): 481–486, figures 1–5.

1918. Branchiobdellid Worms (Annelida) from Michigan Crayfishes. *Transactions of the American Microscopical Society,* 37(1): 49–51.

1919. The Branchiobdellid Worms in the Collections of the United States National Museum, with Description of New Genera and New Species. *Proceedings of the United States National Museum,* 55(2267): 241–265, figures 1–18, plates 10–13.

Franzén, Åke

1962. Notes on the Morphology and Histology of *Xironogiton instabilia* (Moore 1893) (fam. Branchiobdellidae) with Special Reference to the

Muscle Cells. *Zoologiska Bidrag från Uppsala,* 35: 369–384, figures 1–4, plates I–IV.

Georgévitch, Jivoin
1955. Sur les Branchiobdellides des ecrivisses du Lac Dojran. *Acta Musei Macedonici Scientiarum Naturalium,* 2(10/21): 199–221, figures 1–33.
1957. Les Branchiobdellides de Yougoslavie. *Bulletin de l'Academie serbe des Sciences,* 18: 7–22, figures 1–33.

Goodnight, Clarence J.
1940. The Branchiobdellidae (Oligochaeta) of North American Crayfishes. *Illinois Biological Monographs,* 17(3): 1–75, plates 1–3.

Hall, Maurice C.
1914. Descriptions of a New Genus and Species of the Discodrilid Worms. *Proceedings of the United States National Museum,* 48(2071): 187–193, figures 1–3.

Henle, G. J.
1835. Ueber die Gattung *Branchiobdella. Archiv fur Anatomie, Physiologie und Wissenschaftliche Medicin,* 1835: 574–608, plate 14.

Hobbs, Horton H., Jr., Perry C. Holt and Margaret Walton
1967. The Crayfishes and their Epizoötic Ostracod and Branchiobedellid Associates of the Mountain Lake, Virginia, Region. *Proceedings of the United States National Museum,* 123(3602): 1–84, figures 1–22.

Hoffman, Richard L.
1963. A Revision of the North American Annelid Worms of the Genus *Cambarincola* (Oligochaeta: Branchiobdellidae). *Proceedings of the United States National Museum.* 114(3470): 271–371, figures 1–79.

Holt, Perry C.
1949. A Comparative Study of the Reproductive Systems of *Xironogiton instabilius instabilius* (Moore) and *Cambarincola philadelphica* (Leidy) (Annelida, Oligochaeta, Branchiobdellidae). *Journal of Morphology,* 84(3): 535–572, plates 1–4.
1951. The Genera *Xironodrilus* and *Pterodrilus* in North America with Notes on other North American Genera of the Family Branchiobdellidae (Annelida, Oligochaeta). Unpublished dissertation, University of Virginia, 1–241, plates 1–30.
1953. Characters of Systematic Importance in the Family Branchiobdellidae (Oligochaeta). *The Virginia Journal of Science, New Series,* 4(2): 57–61.
1960. The Genus *Ceratodrilus Hall* (Branchiobdellidae, Oligochaeta) with the Description of a New Species. *The Virginia Journal of Science, New Series,* 11(2): 53–77, plates 1–4.
1964. The Distribution of the Branchiobdellids: Some Zoogeographical Problems. *American Zoologist,* 4(4): 260. (Abstract).
1965. On *Ankyrodrilus,* a New Genus of Branchiobdellid Worms (Annelida). *The Virginia Journal of Science, New Series,* 16(1): 9–21, figures 1–14.
1967. Status of the Genera *Branchiobdella* and *Stephanodrilus* in North America with Description of a New Genus (Clitellata: Branchiobdellida). *Proceedings of the United States National Museum,* 124(3631): 1–10, figures 1–4.
1968a. The Branchiobdellida: Epizoötic Annelids. *The Biologist,* 50(3–4): 79–94, figures 1–2.
1968b. New Genera and Species of Branchiobdellid Worms (Annelida: Clitellata). *Proceedings of the Biological Society of Washington,* 81:291–318, figures 1–9.
1968c. The Genus *Pterodrilus* (Annelida: Branchiobdellida). *Proceedings of the United States National Museum,* 125(3668): 1–44, figures 1–12.
1969. The Relationships of the Branchiobdellid Fauna of the Southern Appalachians. (in) Holt, Perry C., ed., *The Distributional History of the Biota of the Southern Appalachians, Part I, Invertebrates.* Virginia Polytechnic Institute, Research Division Monograph 1: 191–219, figures 1–10.

Leidy, Joseph
1851. Contributions to Helminthology. *Proceedings of the Academy of Natural Sciences of Philadelphia,* 5: 205–209.

McManus, Lawrence R.
1960. Some Ecological Studies of the Branchiobdellidae (Oligochaeta). *Transactions of the American Microscopical Society,* 79(4): 420–428.

McKenzie, Dan P.
1972. Plate Tectonics and Sea Floor Spreading. *American Scientist,* 60(4): 425–435.

Moore, J. Percy
1894. On Some Leech-like Parasites of American Crayfishes. *Proceedings of the Academy of Natural Sciences of Philadelphia,* (for 1893): 419–428, plate 12.
1895. The anatomy of *Bdellodrilus illuminatus,* an *American discodrillid. Journal of Morphology,* 10(2): 497–540, plates 28–32.

Odier, Auguste
1823. Mémoire sur le Branchiobdelle, Nouveau Genre d' Annelides de la Famille des Hirudinees. *Mémoires de la Societe d' Histoire Naturelle de Paris,* 1:71–78, plate 4.

Pennak, Robert W.
1953. Fresh-water Invertebrates of the United States. The Ronald Press Company, New York, ix + 769.

Pierantoni, Umberto
1965. *Cirrodrilus cirratus,* n.g., n. sp. parassita del' *Astacus japonicus. Annuario del Museo Zoologico della (R. Universita) di Napoli (Nuova Serie),* 2(11): 1–9.
1912. Monografia dei Discodrilidae. *Annuario del Museo Zoologico (R. Universitaí di Napoli (Nuova Serie),* 3(24): 1–28, figures 1–20, plate 5.

Pop, Victor
1965. Systematische revision der europäischen Branchiobdelliden (Oligochaeta). *Zoologische Jahrbuch für Systematik,* 92: 219–238, figures 1–12.

Smallwood, W. M.
1906. Notes on *Branchiobdella. Biological* Bulletin, 11: 100–111.

Stephenson, J.
1930. The Oligochaeta. University Press, Oxford, xiv, 978.

Whitman, C. O.
1882. A New Species of *Branchiobdella. Zoologischer Anzeiger,* 3(4): 636–637.